Oxygen consumption by and blood flow across the portal-drained viscera and liver of pregnant ewes

H. C. Freetly and C. L. Ferrell

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Oxygen Consumption by and Blood Flow Across the Portal-Drained Viscera and Liver of Pregnant Ewes[1]

H. C. Freetly and C. L. Ferrell

USDA, ARS, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933

ABSTRACT: The energy requirement of ewes increases during pregnancy. In late pregnancy, approximately 40% of the increase in heat production can be attributed to increases in heat production by nonreproductive tissues. The objective of this study was to determine the pattern of oxygen consumption by the portal-drained viscera (PDV) and liver during pregnancy to allow for an estimation of the extent to which these tissues contribute to the increase in energy requirement. Nineteen multiparous ewes were individually penned and allowed ad libitum access to an alfalfa hay-based diet. Catheters were surgically placed in the portal vein, a branch of the hepatic vein, a mesenteric vein, and the abdominal aorta. Oxygen consumption by the PDV and liver were subsequently measured before breeding and at 6, 19, 39, 61, 82, and 103 d before lambing. Hepatic arterial blood flow was not influenced by litter size (P = .89) or stage of pregnancy (P = .28). Portal and hepatic venous blood flow peaked 19 d before lambing. Oxygen consumption by the PDV and liver increased with increased ad libitum feed intake. The increase in hepatic oxygen consumption occurred approximately 63 d earlier in ewes with twins than in ewes with a single fetus independent of changes in feed intake. Hepatic oxygen consumption increased with duration of gestation and was estimated to account for 40% of the heat production not associated with the gravid uterus.

Key Words: Sheep, Pregnancy, Metabolism, Liver, Blood Flow

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Introduction

Energy requirements of ewes increase 50 to 120% over maintenance at the end of pregnancy, depending on litter size (NRC, 1985). The increase in energy demand during pregnancy is required to support conceptus growth, support growth of nonreproductive tissues, and maintain requirements of the conceptus and ewe. The proportion of retained energy deposited in extrauterine tissues is dependent on level of feed intake (Rattray, 1974a). In well-fed ewes, the empty body retains approximately 87% of the retained energy, compared to 13% in the gravid uterus (Rattray, 1974a). At 90 d of gestation, the contribution of the increase in maternal tissues to the increase in heat production has been estimated to be 32% (Bell, 1986). Limited information is available on the relative contribution of different maternal tissues to the increase in heat production. The objective of this study was to determine the pattern of oxygen consumption by the portal-drained viscera (**PDV**) and liver during pregnancy to allow for an estimation of the extent to which these tissues contribute to the increase in energy requirement.

Materials and Methods

Animal Management

Nineteen multiparous polled Dorset ewes (76 ± 1 kg) that had previously exhibited behavioral estrus were housed in individual pens (1.17 m^2). Ewes were walked 905 m on each Monday, Wednesday, and Friday. Room temperature was kept at 20°C with a light:dark cycle of 12:12 h. Lights came on at 0630. Sheep had ad libitum access to water and a pelleted diet (57% dehydrated alfalfa, 28% corn cobs, and 15% corn as fed). Ewes were adapted to the diet 58 d before the first blood samples were collected. Ewes were fed daily at 1300, and feed refusal from the previous day was determined at feeding.

Catheters were surgically placed in the portal vein, a branch of the hepatic vein, a mesenteric vein, and the abdominal aorta as described by Ferrell et al. (1992). Twenty-four days following surgery, a progesterone-releasing intravaginal device (**PRID**) was inserted into the ewes and left for 14 d. Fourteen

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days following removal of the PRID, ewes were grouped in pens of five and exposed to one ram for nine consecutive days. Rams were rotated between pens every 24 h. Marking harnesses were placed on rams, and tup marks were recorded. At the end of the breeding period, ewes were returned to their individual pens. It was the intent of the study to create three treatments: nonpregnant ewes, ewes with a single pregnancy, and ewes with a twin pregnancy. Experimental procedures were conducted in accordance with the Meat Animal Research Center Animal care guidelines and the *Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching* (Consortium, 1988).

Sample Protocol

Seven days following removal of the PRID, ewes were transferred to a metabolism crate (151 d prepartum). A priming dose (15 mL) of *P*-aminohippuric acid (.15 *M*; **PAH**) was given via the mesenteric vein, followed by a constant infusion (.8 mL/min) of PAH. Sixty minutes following the priming dose, blood samples were drawn into heparinized syringes (10 mL) and EDTA-containing syringes (5 mL) from the aortic, portal venous, and hepatic venous catheters. Samples were collected at 30-min intervals for a total of seven sets of samples per period (aortic, portal venous, and hepatic venous). An additional 1.0 mL of blood was drawn into heparinized syringes and analyzed immediately for hemoglobin and percentage of oxygen saturation of hemoglobin (Hemoximeter, Model OSM-2, Radiometer America, Westlake, OH). Additional samples were collected as above 6, 19, 39, 61, 82, and 103 d before parturition.

Fresh blood samples for PAH analysis were diluted 1:4 (vol:vol) with deionized water. Blood samples were analyzed for PAH by automated procedures (Technicon Industrial Systems, 1972 No. 216–72T). Oxygen concentrations were calculated as described by Burrin et al. (1989).

Blood flow was calculated using an indicator-dilution technique previously described (Katz and Bergman, 1969). Net fluxes of oxygen were calculated by multiplying blood flow by the concentration difference in the vessels (Katz and Bergman, 1969).

Feed Energy

Apparent digestibility of the feed was determined in six polled Dorset wether lambs that had been raised in the same facility in which the ewes were housed. Lambs had ad libitum access to the same diet before and after weaning. Lambs were 95 ± 2 d of age and had a BW of 30.2 ± 2.0 kg at the start of the collection period. Total feed intake and fecal output were determined over a 96-h period. Fresh feed was offered daily and offered feed exceeded 25% of the daily feed intake. Feces were collected in a canvas bag. Feces were collected daily, and a 20% subsample was collected and frozen. Subsamples were combined to form a single composite sample. Feed and fecal samples were dried at 55°C and ground to pass through a 1-mm screen. Gross energy content (Mcal/kg) of feed and feces was determined by bomb calorimetry (AOAC, 1984). Apparent digestible energy content of the feed was calculated as the gross energy of consumed feed minus the gross energy in the feces divided by feed intake. Digestible energy intake was calculated as the product of the feed DE times feed intake.

Data were analyzed as a split-plot in time with SAS (1989) GLM procedures. Differences between means were tested with a linear model that included animal, litter size, and period as discrete effects. The model was litter size, animal nested within litter size, period, and litter size by period. Litter size means were tested with animal nested within litter size as the source of error. Means and standard errors are presented in the text, tables, and figures. For the sake of discussion, responses with probabilities less than .05 are considered to be different.

Results

Feed Energy

Feed intake during the 96-h collection period was 4.984 ± .245 kg. The feed contained 90.8% DM and had a gross energy content of 4.362 Mcal/kg of DM. Energy had an apparent digestibility of .53 ± .01. Apparent digestible energy concentration of the diet on an as-fed basis was 2.09 ± .04 Mcal/kg of feed.

Pregnant Ewes

Two ewes did not give birth to lambs (**Nonpregnant**). Six ewes gave birth to a single lamb (**Single**), and 11 ewes gave birth to twins (**Twin**). One ewe in the Single group had a catheter in the hepatic vein that failed to bleed during Periods 5 and 7. In the Twin group, one ewe was removed from study after Period 3, and a second ewe was removed after Period 4 due to failure of the abdominal aortal catheter. One ewe in the Twin group lambed before Period 7 and therefore was not sampled during Period 7. Ewes with missing data were included in data analysis.

Gestation length calculated as days from first tup mark to parturition did not differ between ewes with single (143.7 ± 1.0 d) or twin (142.0 ± 1.4 d) litters (P = .43). At birth, lambs born as twins (3.50 ± .16 kg) weighed less than lambs born as a single (4.79 ± .22 kg; P < .001). The days before birth were determined as the number of days before parturition on the day that the sample was collected. The average number of days before birth for singles was 153 ± 2, 104 ± 2, 82 ± 1, 62 ± 1, 40 ± 1, 20 ± 1, and 6 ± 1 for

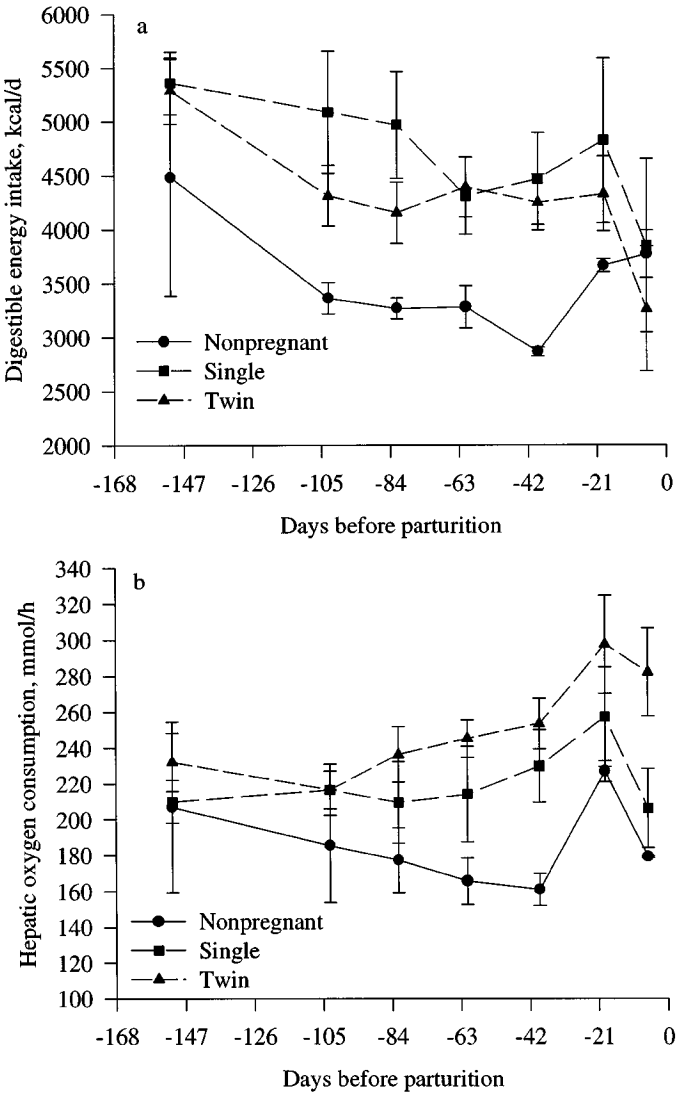

Figure 1. (a) Means and standard errors for digestible energy intake of pregnant ewes. (b) Means and standard errors for hepatic oxygen consumption of pregnant ewes. Nonpregnant ewes (n = 2). Single: –151 to –61 d and –19 d (n = 6); –39 and –6 d (n = 5). Twin: –151 to –82 d (n = 11); –61 d (n = 10), –39 and 19 d (n = 9); –6 d (n = 8).

Periods 1 through 7, respectively. The average number of days before birth for twins was 151 ± 2, 102 ± 1, 82 ± 1, 60 ± 2, 39 ± 2, 19 ± 1, and 6 ± 1 for Periods 1 through 7, respectively. Because nonpregnant ewes did not give birth, the days from birth were calculated based on mating date and the gestational length of ewes that gave birth to single lambs.

From Period 1 to 7, BW increased 6.6 kg in the Nonpregnant group, 18.1 kg in the Single group, and 18.6 kg in the Twin group (Table 1). Feed and DE intake tended to decrease during the experiment (Table 1; Figure 1).

Hepatic arterial blood flow did not differ with litter size or over time (Table 1). Portal venous blood flow decreased over time in the nonpregnant ewes and peaked during Period 6 in the pregnant ewes (Table 1). Hepatic venous blood flow followed a pattern similar to portal venous blood flow (Table 1).

Arterial oxygen concentration was not affected by litter size or stage of pregnancy (Table 1). Arterial-portal venous oxygen concentration difference (1.45 ± .24 mmol/h) was not affected by litter size (P = .92) or by stage of pregnancy (P = .96). Arterial-hepatic venous oxygen concentration difference (2.50 ± .30 mmol/L) was not affected by litter size (P = .53) or by stage of pregnancy (P = .82). Similarly, portal-hepatic venous oxygen concentration difference (1.05 ± .13 mmol/L) was not affected by litter size (P = .31) or by stage of pregnancy (P = .42).

Portal-drained viscera oxygen consumption followed a pattern similar to that of portal venous blood flow (Table 1). Hepatic oxygen consumption was increased with increased litter size and peaked during Period 6 (Figure 1). Like hepatic oxygen consumption, total splanchnic oxygen consumption peaked during Period 6 (Table 1).

The relationship between PDV and liver oxygen consumption and level of ad libitum feed intake was determined by regressing PDV and liver oxygen consumption during Period 1 on feed intake. Portal-drained viscera oxygen consumption increased linearly with increased feed intake. The regression had a slope of .057 ± .015 and an intercept of 104.30 ± 39.21; R^2 = .45. Like PDV, hepatic oxygen consumption increased linearly with increased feed intake. The regression had a slope of .057 ± .021 and an intercept of 80.90 ± 52.49; R^2 = .31. The change in hepatic oxygen consumption beyond that due to changes in feed intake was calculated as the difference between observed rates of oxygen consumption minus the hepatic oxygen consumption predicted by feed intake (Figure 2). In the Single group, the change in hepatic oxygen consumption did not differ from zero except at 19 d before birth (P = .05). In the Twin group the change in hepatic oxygen consumption differed from zero (P < .05) starting 82 d before birth.

Discussion

The energy requirements of ewes increase as pregnancy advances (Graham, 1964; Langlands and Sutherland, 1968; Rattray et al., 1974a). The increase in energy requirement above maintenance generally follows an exponential increase. Fetal growth follows a similar pattern (Koong et al., 1975); however, the increase in energy required during pregnancy is not solely associated with energy deposition in the gravid uterus.

The additional energy required during pregnancy can be divided into four general categories: energy retained in the gravid uterus, energy retained by the ewe, heat produced by the gravid uterus, and increased maternal heat production. Energy retained in

Table 1. Means and standard errors for blood flow through and oxygen consumption by the portal-drained viscera and liver of pregnant ewes[a]

Item and litter size	Period							Probability		
	1	2	3	4	5	6	7	Litter	Period	L × P
Days before parturition	151 ± 1	103 ± 1	82 ± 1	61 ± 1	39 ± 1	19 ± 1	6 ± 1			
Body weight, kg								.14	.003	.997
0	74.1 ± 6.5	77.9 ± 6.7	78.5 ± 7.3	80.9 ± 6.6	81.1 ± 6.0	79.7 ± 4.5	80.7 ± 5.0			
1	79.3 ± 4.2	85.8 ± 4.5	89.3 ± 4.3	91.8 ± 5.1	94.6 ± 4.9	95.3 ± 5.3	97.4 ± 6.5			
2	75.2 ± 1.9	81.8 ± 2.0	85.4 ± 1.9	89.8 ± 2.0	92.8 ± 2.8	93.1 ± 3.2	93.8 ± 3.4			
Feed intake, g/d								.12	.11	.96
0	2,147 ± 526	1,610 ± 69	1,565 ± 47	1,571 ± 94	1,372 ± 20	1,756 ± 29	1,807 ± 106			
1	2,565 ± 140	2,436 ± 273	2,380 ± 238	2,064 ± 171	2,140 ± 203	2,312 ± 366	1,845 ± 386			
2	2,530 ± 148	2,065 ± 135	1,990 ± 136	2,104 ± 133	2,036 ± 124	2,074 ± 166	1,563 ± 166			
Blood flow, L/h								.89	.28	.96
Hepatic arterial										
0	15.3 ± 8.7	9.1 ± 1.3	25.3 ± 3.4	11.8 ± 9.3	31.2 ± 2.0	37.7 ± .7	24.9 ± 6.3			
1[b]	14.6 ± 2.8	23.2 ± 6.6	21.2 ± 3.9	26.9 ± 3.1	28.3 ± 8.0	26.6 ± 6.7	20.9 ± 8.2			
2	23.2 ± 3.3	28.5 ± 5.6	32.2 ± 4.7	28.4 ± 3.8	29.7 ± 4.8	31.4 ± 10.0	31.0 ± 4.3			
Portal venous								.04	.006	.36
0	170.5 ± 29.1	194.3 ± 47.8	122.3 ± 19.6	131.6 ± 24.0	89.5 ± 7.6	150.8 ± 4.4	140.3 ± 17.2			
1	167.6 ± 6.5	158.8 ± 11.9	143.2 ± 5.5	145.8 ± 8.9	154.9 ± 13.4	170.9 ± 12.6	153.5 ± 12.9			
2	169.7 ± 8.8	154.8 ± 9.9	146.2 ± 9.2	150.5 ± 10.0	156.2 ± 8.7	193.9 ± 16.0	172.4 ± 9.7			
Hepatic venous								.16	.007	.50
0	185.7 ± 20.4	203.3 ± 46.5	147.5 ± 16.2	143.4 ± 14.7	120.7 ± 9.7	188.5 ± 5.1	165.1 ± 10.9			
1[b]	182.2 ± 6.6	181.9 ± 7.0	164.3 ± 4.4	172.6 ± 11.0	176.3 ± 15.7	197.5 ± 15.0	162.2 ± 13.0			
2	192.9 ± 9.9	183.3 ± 9.1	178.4 ± 10.1	178.8 ± 7.3	185.9 ± 6.8	225.3 ± 16.9	203.4 ± 11.0			
Oxygen concentration, m*M*										
Arterial								.29	.58	.41
0	6.57 ± .36	6.42 ± .28	6.08 ± .12	5.95 ± .00	5.89 ± .30	6.14 ± .37	6.06 ± .23			
1	6.37 ± .14	6.15 ± .11	6.02 ± .08	5.99 ± .12	6.14 ± .15	6.28 ± .18	6.69 ± .14			
2	6.48 ± .13	6.45 ± .16	6.73 ± .17	6.67 ± .19	6.60 ± .17	6.62 ± .16	6.71 ± .13			
Oxygen consumption, mmol/h										
Portal-drained viscera								.26	.10	.81
0	261.8 ± 63.3	279.2 ± 83.7	184.6 ± 22.7	181.9 ± 32.7	119.6 ± 12.0	233.9 ± 19.0	199.4 ± 21.4			
1	255.6 ± 10.1	229.3 ± 24.2	219.9 ± 13.1	222.0 ± 16.7	236.3 ± 31.5	280.4 ± 36.3	232.5 ± 40.6			
2	241.1 ± 12.0	213.5 ± 19.9	207.2 ± 20.8	219.7 ± 13.7	229.3 ± 17.0	261.5 ± 27.4	233.1 ± 22.5			
Hepatic								.04	.19	.91
0	206.9 ± 47.7	185.3 ± 31.6	177.2 ± 18.2	165.6 ± 13.0	160.9 ± 9.0	226.8 ± 5.8	178.9 ± .5			
1[b]	210.0 ± 12.0	216.6 ± 10.5	209.5 ± 23.0	214.0 ± 26.8	229.7 ± 20.2	257.0 ± 27.5	206.1 ± 22.1			
2	232.2 ± 16.2	216.6 ± 14.3	236.3 ± 15.5	245.1 ± 10.4	253.3 ± 14.1	297.3 ± 27.2	281.8 ± 24.3			
Splanchnic								.06	.02	.70
0	468.7 ± 111.0	464.6 ± 115.3	361.8 ± 40.9	347.4 ± 45.7	280.5 ± 20.9	460.7 ± 24.8	378.3 ± 20.9			
1[b]	465.6 ± 15.7	445.8 ± 29.5	429.4 ± 33.3	435.9 ± 42.6	449.7 ± 38.2	537.4 ± 60.5	403.3 ± 39.0			
2	473.3 ± 26.2	430.1 ± 29.9	443.4 ± 33.3	464.8 ± 18.0	482.6 ± 23.2	558.8 ± 47.9	514.9 ± 42.6			

[a]Litter size 0 (n = 2); litter size 1 (n = 6); and litter size 2, Period 1 to 3 (n = 11); Period 4 (n = 10); Period 5 to 6 (n = 9); and Period 7 (n = 8).
[b]Litter size 1, Period 5 and 7 (n = 5).

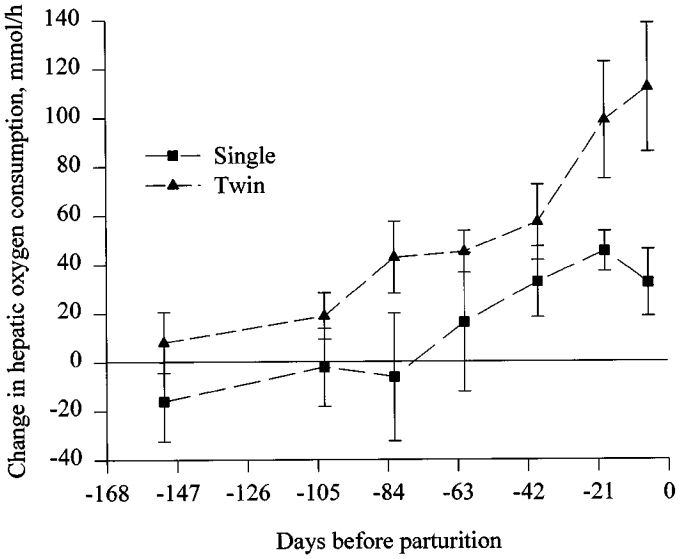

Figure 2. Means and standard errors for changes in hepatic oxygen consumption corrected for feed intake. Nonpregnant ewes (n = 2). Single: –151 to –61 d and –19 d (n = 6); –39 and –6 d (n = 5). Twin: –151 to –82 d (n = 11), –61 d (n = 10), –39 and 19 d (n = 9); –6 d (n = 8).

the conceptus is less than that retained in maternal tissues (Langlands and Sutherland, 1968; Rattray et al., 1974a).

The increase in heat production is the sum of the heat produced by the gravid uterus and the increase in heat produced by maternal tissues, in which metabolic rates have responded to support the pregnancy. This latter component can be termed the maternal component. Ferrell and Reynolds (1985) suggested that the increase in heat production of the gravid uterus in cattle accounts for approximately 44% of the increase in total heat production. Bell (1986) calculated that the contribution of the gravid uterus in sheep to the increase in heat production was 79%. In late pregnancy, a ewe with a single fetus increases her heat production by 17 to 29% (Graham, 1964; Guerouali et al., 1991). In the current study, Nonpregnant ewes had reached weight stasis (80.6 kg) in Period 4 to 7 and had an ME intake of 2,786 kcal/d. We estimated that heat production was 104 (kcal/kg$^{.75}$)/d. If one assumes that heat production increases 22% by 19 d before lambing, there would be a 613 kcal/d increase in heat production. Based on slaughter data (Rattray et al., 1974b; Koong et al., 1975), the weight of the gravid uterus 19 d before birth was calculated to be 4.84 kg and an oxygen consumption rate of 550 mmol/kg·d^{-1} was used (Caton et al., 1979). If we assume that 113 kcal/mol oxygen is produced, the heat produced by the gravid uterus contributes 49% toward the increase in heat production. The above finding indicates that in sheep and cattle the maternal contribution to the increase in heat production is 51 to 56%.

In cows, glucose uptake by the gravid uterus increases from .58 mmol/min in midpregnancy (d 137) to 2.61 mmol/min in late pregnancy (d 250; Ferrell and Reynolds, 1985). In ewes in late pregnancy, glucose uptake by the gravid uterus has been reported to be 16.8 mmol/h (Battaglia and Meschia, 1981). In ruminants, the liver is the primary source of blood glucose, suggesting that liver energy expenditure would increase and contribute to the increase in the maternal component. Fell et al. (1972) found the intestinal mucosal weight did not change during late pregnancy; however, liver weights increased. The increase in liver weight during late pregnancy observed by Fell et al. (1972) was accompanied by an increase in total liver glucose-6-phosphatase and fructose-1,6-diphosphatase activity (Mackie et al., 1972), suggesting that total metabolic activity is increased as well.

In our experiment, blood oxygen concentration differences between vessels did not change with stage of pregnancy. Oxygen consumption by the tissues followed the same pattern as blood flow to the tissues. Rosenfeld et al. (1977) reported that cardiac output increased from 289 L/h in nonpregnant ewes to 510 L/h in late-pregnant ewes and that blood flow to reproductive and nonreproductive tissues increased. As in the current study, Rosenfeld et al. (1977) did not observe a change in the arterial blood flow to the liver in pregnant ewes. Even though arterial blood flow to the liver did not change, portal venous blood flow increased in late pregnancy in this study.

Forbes (1970) found that feed intake decreased as pregnancy progressed in ewes, and the pattern is the same as that observed in the current study. The week before parturition, feed intake in the pregnant ewes tended to decrease to its lowest level. This decrease in feed intake probably led to the decrease in portal venous blood flow and hepatic oxygen consumption observed just before parturition. Previous studies have demonstrated that reduced feed intake results in a decreased PDV and hepatic oxygen consumption in growing lambs (Burrin et al., 1989; Freetly et al., 1995). These studies were based on lambs that were feed-restricted; however, the relationship between feed intake and oxygen consumption was maintained in the current study when nonpregnant ewes were given ad libitum access to feed. Even though feed intake tended to decrease over the pregnancy, hepatic oxygen consumption increased as pregnancy progressed. The increase in hepatic oxygen consumption associated with maintaining pregnancy becomes a large proportion of the total hepatic oxygen consumption after variation due to feed intake is subtracted (Figure 2). At 19 d before birth, the proportion associated with singles was .18 and that associated with twins was .33. Based on the hepatic oxygen consumption rates adjusted for feed intake it seems that twin pregnancies result in increased hepatic aerobic activity 63 d earlier than single pregnancies.

Based on the assumption that the gravid uterus contributed 49% toward the increase in heat production, we estimated that 312 kcal/d of the increase in heat production was derived from the maternal component 19 d before birth. In the current study, hepatic oxygen consumption in ewes with a single lamb increased 1.128 mol/d. If we assume that 110 kcal/mol of oxygen was produced, the liver contributed 20% toward the increase in heat production or 40% toward the maternal component. The changes in energy expenditure by the liver represent the sum of the decreased energy expenditure associated with decreased feed intake and the increased energy expenditure associated with the support of the pregnancy.

In conclusion, PDV and hepatic oxygen consumption in ewes with ad libitum access to feed increases with feed intake. Hepatic oxygen consumption increases in pregnant ewes. Aerobic liver metabolism is a principal contributor to the maternal component of the increase in heat production. Increases in hepatic oxygen consumption occur relatively early (~61 d of gestation) in ewes with twins compared to those with singles (~124 d of gestation), suggesting that differences in nutrition management between ewes with different litter sizes may need to begin in advance of the third trimester. Even though the liver contributes to a large fraction of the maternal component, other tissues clearly contribute. Increases in cardiac output suggest an increase in energy expenditure by the heart (Rosenfeld, 1977). In late pregnancy, the mammary gland gains 62 g/d of fat and 13.5 g/d of protein. In addition, blood flow to the mammary gland increased 161.4 mL/min in late pregnancy, (130 to 140 d) over nonpregnant ewes (10.6 mL/min; Rosenfeld, 1977) suggesting that the mammary gland may contribute to the maternal component.

Implications

Oxygen consumption by the liver is a good indicator of the energy requirement of ewes. Ewes require more feed to support pregnancy as pregnancy progresses. This study suggests that the nutrient requirement of ewes with twin fetuses increases 63 d earlier than in ewes with single fetuses. These findings imply that early diagnosis of fetal number will allow for strategic feeding of pregnant ewes, which in turn should reduce feed costs.

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